

HOST-PARASITE INTERACTIONS OF BROWN-HEADED COWBIRDS AND DARK-EYED JUNCOS IN VIRGINIA

LICIA WOLF¹

ABSTRACT.—In the Allegheny mountains of Virginia, 39% of Dark-eyed Junco (*Junco hyemalis*) nests contained at least one Brown-headed Cowbird (*Molothrus ater*) egg. Cowbirds laid an average of 1.7 eggs in each nest, and they removed an average of 1.2 junco eggs/nest. Removals primarily accounted for the reduction in mean number of junco young that were hatched and fledged in parasitized compared to nonparasitized broods. The majority of cowbird eggs were laid during the juncos' laying period, although some were laid slightly before or after the juncos' laying period. Most junco nestlings in nests with one cowbird nestling grew nearly as well as did those without cowbirds. Nest predation during incubation was higher in parasitized nests only in one of two years. Junco nests in relatively open areas appeared to have been more conspicuous both to cowbirds and predators. Brown-headed Cowbirds are recent invaders in this area, and possible antiparasite adaptations are discussed. Received 7 Nov. 1985, accepted 12 Jan. 1987.

Brown-headed Cowbirds (*Molothrus ater*) are opportunistic parasites that lay their eggs in the nests of many species (Southern 1958, Mayfield 1965, Friedmann et al. 1977). Some hosts (e.g., *Empidonax* spp. [Walkinshaw 1961], *Sayornis phoebe* [Rothstein 1975a]) suffer extreme reduction in reproductive success when one or more cowbird nestlings are present in the nest. Other species (e.g., *Melospiza melodia* [Nice 1937], *Seiurus aurocapillus* [Hann 1937]) are able to raise most of their own young in the nest along with cowbird young. The degree to which host nestmates can or cannot survive appears to be affected by the relative lengths of incubation of the cowbird and its host (Hann 1937, Payne 1977).

Host species often suffer clutch reduction due to the removal of and damage to eggs by cowbird females (Hann 1941, Carey 1986). In addition, cowbird nestlings have higher growth rates and attain a larger final size than the nestlings of many hosts (Hann 1937, Nolan 1978, Wiley 1986).

This study reports Brown-headed Cowbird parasitism of the Dark-eyed Junco (*Junco hyemalis carolinensis*) in the Allegheny Mountains of Virginia. Juncos are primarily ground-nesting and usually build their nests in road cuts or creek banks, often in edge habitats. Junco eggs in Virginia normally hatch after 12-13 days of incubation (Hostetter 1961, pers. obs.) vs 11 days for the cowbird. Juncos are able to raise some of their own

¹ Dept. Biology, Indiana Univ., Bloomington, Indiana 47405.

nestlings with cowbird nestlings (White 1973). Because cowbirds have been present in this area only for about 20 years (D. W. Johnston, pers. comm.), the interactions of these species are of special interest in view of host-parasite coevolution.

STUDY AREA AND METHODS

The study was conducted within a 3.5-km radius of Mountain Lake Biological Station (MLBS), Giles County, Virginia, elevation 1198 m, between 17 May and 5 August 1983, and 9 May and 15 August 1984. The predominant habitat is deciduous forest, with oak (*Quercus* spp.), maple (*Acer* spp.), and hemlock (*Tsuga* spp.), interspersed with small fields and human settlements.

Junco nests were found during all stages of the nesting cycle and thereafter visited daily between 12:00 and 18:00 h. Junco and cowbird nestlings were weighed with a 10-g or 50-g Pesola spring scale to the nearest 0.1 g. Nestlings were not weighed after they reached eight days of age to prevent premature fledging. Some young were also weighed upon fledging.

Cowbird parasitism rates were calculated by determining the percent of active junco nests in which at least one cowbird egg was laid; active nests are those that were known to have been attended by a junco female the day before the junco would have, or had, laid her first egg. Because cowbird females occasionally remove cowbird eggs from nests (Nolan 1978: 377), nests that I found after the onset of junco laying may be subject to a bias of fewer cowbird eggs per nest (Rothstein 1975b). I was less attendant to individual cowbird eggs in 1983 than I was in 1984. In 1984 all eggs were marked on the day of laying, and individual eggs were closely monitored. I therefore included only the data from 1984 in the analysis of the number of cowbird eggs removed from junco nests.

Although I did not directly observe more than one cowbird parasitizing the same junco nest, I was fairly certain it occurred when two or more cowbird eggs appeared in a nest in one day, or when cowbird eggs in a nest were extremely different in size (cf. Friedmann 1929, Nice 1937:156, Hoy and Ottow 1964, McGeen and McGeen 1968, Dufty 1983).

In nests for which I did not know the exact date a cowbird egg was laid (e.g., if the nest was found after clutch completion), I estimated the approximate date of laying by backdating from the hatching date (assuming an eleven-day incubation period). If the nest failed prior to hatching, I estimated the date the cowbird egg was laid by assuming that it was laid within the first 3 days of the junco's 3–4 day laying period.

I examined selection of host nests by cowbirds with respect to the conspicuousness of nests by dividing the study area into two major vegetation zones or "habitat types" that may have influenced the cowbirds' ability to locate and parasitize junco nests. The first, designated "closed canopy," was along a rarely traveled dirt road that followed a canyon stream through relatively dense secondary riparian deciduous forest. The other, designated "open canopy," included all remaining sites in the study area, none of which included dense forest. To determine whether nests in open habitats were more likely to be found by cowbirds, predators, or both, I compared parasitism and predation rates of nests in both habitat types using chi-square analyses. I assumed that a nest was lost to a predator when (1) all eggs disappeared between daily nest checks or (2) I found shell remnants around the nest site. Nests that were known to have failed due to human interference (e.g., desertion of a nest during road construction near the nest) were excluded from the analyses.

In 1984 I removed cowbird eggs from nests in order to standardize junco clutch sizes for a separate study. If nests were found before clutch completion, I removed the junco eggs each day during the laying period and substituted them with cowbird or supplementary junco eggs. The full junco clutch (3–4 eggs) was replaced at the onset of incubation. Most

of the manipulated clutches in 1984 contained at least one junco and one cowbird egg during the laying period. Nests that contained only cowbird eggs were excluded from the analysis of number of junco eggs removed. Because cowbird females were prevented from removing junco eggs in 1984, the analysis of junco clutch size (resulting from potential cowbird interference) includes only data from 1983.

In 1983 I removed cowbird eggs and hatchlings so that only a single cowbird nestling remained in junco nests. Nestling growth is reported only for 1983. This study was carried out simultaneously with a study involving parental care in the Dark-eyed Junco, in which males were removed from some nests and not from others. Consequently, some cowbird young were raised in broods cared for by single female juncos, while others were raised by two parents. I therefore examine growth of cowbird and junco nestlings in broods raised by one parent, two parents, and with pooled data from all nests.

Nestling growth analysis.—I obtained 9 age-specific weights of individual nestlings during the period from hatching (day 0) to day 7 and at fledging (day 10 to day 11 for cowbirds, and day 10 to day 12 for juncos). For juncos, weights were analyzed in two ways: (1) individual weights of nestlings were combined among broods; individual nestlings were the sample unit (for ANOVA on junco nestling growth), and (2) the mean weight for each brood was obtained by calculating the mean weight of nestmates at the same age; the brood was the sample unit (for *t*-tests between parasitized and nonparasitized broods). The former method satisfies the assumption of homogeneous variances between groups, whereas the latter method satisfies the assumption of independence of samples for parametric statistics (e.g., broodmates may be more similar to each other than to nestlings in other broods) (Sokal and Rohlf 1981). I performed ANOVA tests on junco nestling weight for ages day 6, 7, and fledging (day 11–12), in which 3 independent variables were considered: cowbird (presence or absence in nest), male junco (presence or absence), and hatching date.

RESULTS

Seasonal variation in parasitism.—Parasitism in junco nests was highest during May in both years (Fig. 1). Thirty-five percent of 72 nests were parasitized in 1983, and 42% of 103 nests were parasitized in 1984. Parasitism declined to about 17% in late June. In both years, about 92% of the parasitism had occurred by late June; by mid-July cowbird eggs ceased to appear in nests, and cowbird adults were seen and heard infrequently.

Number of cowbird eggs in junco nests.—The maximum number of cowbird eggs found in parasitized junco nests was 3 in 1983 ($\bar{x} = 1.4$ eggs/nest) and 6 in 1984 ($\bar{x} = 1.9$ eggs/nest) (Fig. 1). In 1984 most nests contained one cowbird egg, 2 eggs being the next most common. In 1983 one-cowbird-egg nests were relatively more common than in 1984. The frequency distribution of cowbird eggs in junco nests was statistically similar between both years (2 by 4 contingency table, 2 years with 4 categories of egg frequencies; 1, 2, 3, and 4–6 eggs/nest, $\chi^2 = 5.1$, *df* = 3, $P > 0.15$). All clutches that received 3 or more cowbird eggs were laid in May; such nests appeared to contain eggs laid by more than one cowbird female (Fig. 1). I probably underestimated cowbird egg numbers because of the occasional removal of cowbird eggs by cowbirds, which may have gone undetected in 1983. Nests that contained one cowbird egg/nest were

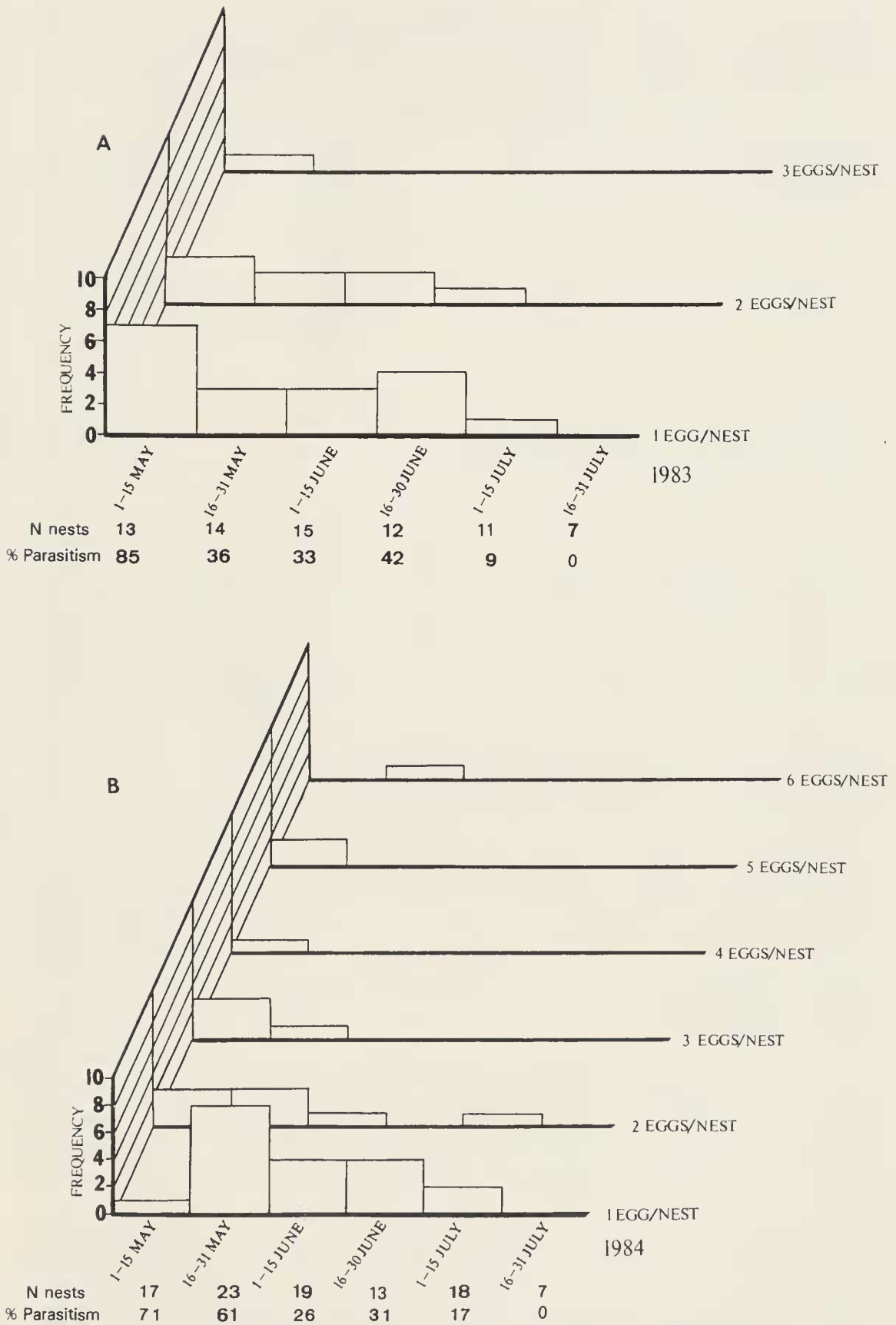


FIG. 1. Number of junco nests containing from one to six cowbird eggs/nest by 2-week increments in 1983 and 1984. Only nests in which the total number of cowbird eggs laid was known are included.

TABLE 1

POISSON DISTRIBUTIONS OF THE NUMBER OF COWBIRD EGGS LAID IN JUNCO NESTS OF ALL NESTS AND ONLY PARASITIZED NESTS, 1983 AND 1984 COMBINED^a

Number of cowbird eggs/nest	Observed frequency ^b	Expected frequency of all nests	Expected frequency of parasitized nests
0	90	76.09	
1	37	54.63	12.07
2	20	19.61	20.51
3	5	4.70	17.43
4	1	0.84	9.89
5	2	0.12	4.20
6	1	0.01	1.43
N		156	66

^a See text for statistics.

^b Includes only clutches laid before 15 July.

less frequent than expected, and those that were not parasitized were more frequent than expected (combining categories of 4–6 eggs/nest, $\chi^2 = 17.6$, $df = 3$, $P < 0.001$) (Table 1). When the distribution of only parasitized nests is examined, however, nests containing one cowbird egg were more frequent than expected ($\chi^2 = 69.7$, $df = 2$, $P < 0.0001$) (Table 1).

In 1984 there were 9 instances in which I was able to document that cowbird eggs were removed from junco nests, presumably by other cowbirds (cf. Hann 1937, 1941), although I did not directly observe cowbirds removing eggs. In 7 of the 9 cases, a new cowbird egg was present at the time I discovered the disappearance of the old egg (or else it had appeared within 2 days), indicating that the nest had been visited by a cowbird. Usually only one egg disappeared a day, leaving the rest of the clutch intact; other evidence (i.e., eventual fledging of the brood) suggested that the egg removals were not due to predators. Removal of eggs by cowbirds is discussed below.

Parasitism in relation to habitat and predation. — In 1984 only, nests in the closed canopy site were parasitized significantly less often than those in the open canopy site (1983: open canopy, 41% parasitized, $N = 44$; closed canopy, 32% parasitized, $N = 28$, $\chi^2 = 0.56$, $P > 0.1$; 1984: open canopy, 45% parasitized, $N = 73$; closed canopy, 20% parasitized, $N = 30$, $\chi^2 = 7.67$, $P < 0.01$).

In 1983 no difference occurred between parasitized and nonparasitized clutches in the proportion of nests in which at least one egg of either species hatched. In 1984, however, significantly more parasitized nests than nonparasitized nests failed during incubation (55 vs 31%; $\chi^2 = 5.41$, $P < 0.05$).

Nest desertions.—Six nonparasitized and 11 parasitized nests were deserted, either because of human disturbance or other unknown factors. Four desertions in nonparasitized nests occurred before any eggs were laid in the nest. One female deserted after laying one egg. Desertions in parasitized nests occurred (1) when a cowbird egg had been laid in the nest before the junco laid ($N = 3$) or (2) when junco eggs were removed from nests ($N = 4$). The latter nests were always deserted before the second day of incubation. Two juncos deserted their nests before clutch completion after I replaced their eggs with cowbird eggs. The remaining 3 nests (one parasitized, two nonparasitized) were probably abandoned as a result of other human disturbance.

Removal of junco eggs by cowbirds.—As in other studies of cowbird parasitism in small hosts, cowbirds usually removed 1–2 eggs/nest (McGeen and McGeen 1968, Nolan 1978, Walkinshaw 1983). In 1983 the mean number of junco eggs removed from parasitized nests was 1.0 egg/nest (0 eggs removed = 42%, 1 egg removed = 20%, 2 eggs removed = 21%, 3 eggs removed = 11%, $N = 19$ nests). In 1984 the mean number of junco eggs removed from parasitized nests was 1.4 eggs/nest (0 eggs removed = 25%, 1 egg removed = 32%, 2 eggs removed = 32%, 3 eggs removed = 7%, 4 eggs removed = 4%, $N = 28$ nests). In 1983 nearly half of the nests had no junco eggs removed, but in 1984 nests with one and two eggs removed were more common. These figures may be influenced partially by my collection of junco eggs and replacement with cowbird eggs.

Timing of junco laying with respect to cowbird laying, egg removal, and final clutch size.—When 1983 and 1984 data are combined, 34% of the cowbird eggs ($N = 14$) were laid prior to the juncos' first egg, 46% ($N = 19$) were laid during the laying period, and 20% ($N = 8$) were laid during incubation.

Removal of eggs from nests by cowbirds apparently occurred throughout the day. One junco egg disappeared from one nest between 10:30 and 14:45 h, another between 10:15 and 11:05 h. A cowbird egg disappeared between 14:00 and 17:00 h.

Final junco clutch size of parasitized and nonparasitized nests was calculated only for 1983 nests. In 1983 the final clutch size of clutches completed before 15 July was significantly smaller for parasitized clutches than it was for nonparasitized clutches (parasitized: $\bar{x} = 3.0$, mode = 3, $N = 13$, nonparasitized: $\bar{x} = 3.3$, mode = 4, $N = 22$, median test; $\chi^2 = 8.33$, $P < 0.025$).

Hatching order.—As I removed all but one cowbird from each junco nest in 1983, the following includes broods with only one cowbird nestling. Of the 11 cowbird eggs present in 1983 nests in which I knew both the date of incubation onset and the hatching date, 9 cowbirds hatched the

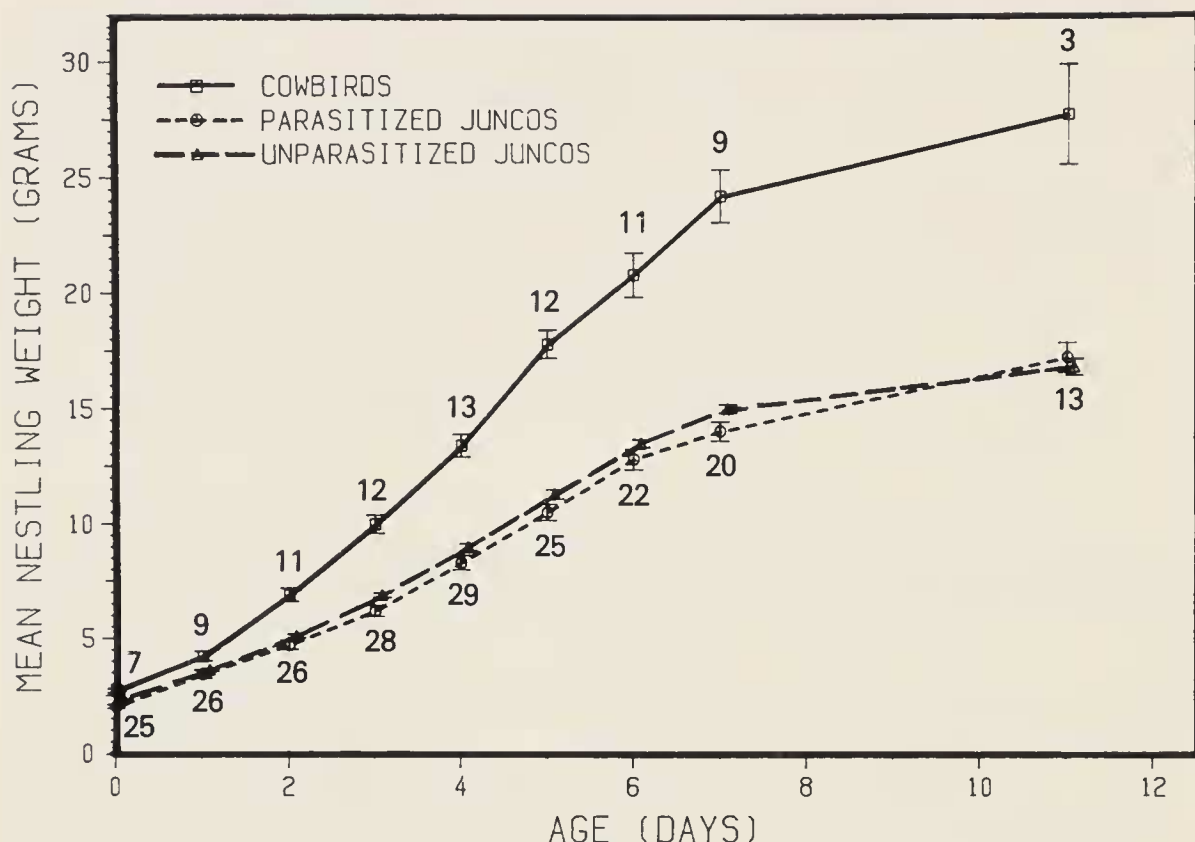


FIG. 2. Growth of cowbird nestlings and junco nestlings in nests with and without cowbirds in 1983. Cowbird weights represent individual nestlings; junco weights are comprised of the mean junco nestling weight in a brood for each age. The number of cowbird nestlings and parasitized junco broods at each age is shown above the cowbird curve. The number of nonparasitized junco broods at each age is shown below the junco curves. Vertical bars indicate ± 1 SE.

day before their junco nestmates, one hatched the same day, and one hatched the day after the first junco nestling. Because of the predominance of earlier hatching by cowbird young, most cowbird nestlings were considerably larger than their junco nestmates (by about 1 g) by the time the juncos hatched (mean hatching-day weight was 2.7 g for cowbirds and 2.3 g for juncos) (Fig. 2). The presence of a single cowbird nestling apparently had no negative effect on junco growth (t -tests between weights of parasitized and nonparasitized juncos, $P > 0.05$).

Influences of parental care and hatching date on nestling growth.—Cowbird young fed by one junco parent were lighter than those fed by two parents, but the samples are too small for statistical analysis (\bar{x} day-7 cowbird weight with one parent = 22.4 g, $N = 4$, \bar{x} day-7 cowbird weight with two parents = 25.7, $N = 5$). Cowbirds in one-parent broods tended to be lighter than those in two-parent broods after day 4. When compared to parasitized juncos in broods with two parents, parasitized junco nest-

TABLE 2
MEAN NUMBER AND PERCENT OF JUNCO YOUNG THAT HATCHED AND FLEDGED IN
PARASITIZED AND NONPARASITIZED NESTS^a

	Number of young hatched	% eggs hatched	Number of young fledged	% hatchlings fledged
Parasitized nests	2.4 ± 0.87 (13) ^b	85	1.5 ± 1.1 (8)	75
Nonparasitized nests	3.3 ± 0.63 (26) ^c	94	2.7 ± 1.1 (12)	82

^a Values were calculated from the number of eggs laid and numbers of young that were present at hatching and fledging.

^b $\bar{x} \pm$ SD (number of nests).

^c One case omitted in which the single cowbird egg was removed before incubation by the investigator.

lings in broods without male care showed depressed growth from about day 3 to day 7. The weight difference ranged from 0.5 to 1.1 g, but these differences are not statistically significant ($P > 0.05$). Both cowbird and junco young of a given age tended to be relatively lighter early in the season (linear regressions with cowbird nestling weight on hatching date for young 3–7 days of age, $P < 0.05$). The correlation of weight with hatching date, however, may be influenced by the relatively greater number of early-season one-parent broods.

Analysis of variance of junco weights on days 6 and 7 showed that nonparasitized and later-season nestlings tended to be heavier (Day 6: overall $F = 7.4$, $P = 0.001$; Day 7: overall $F = 4.6$, $P = 0.002$). Hatching date was the main influence for both ages (partial $P < 0.05$). In addition, there were significant interactions between the variables cowbird and male (partial $P < 0.02$), and between hatching date and male (partial $P = 0.001$). These trends were not apparent at fledging. The analysis indicates that the absence of a male had a negative effect on junco nestling growth, but that this effect was confounded by the negative effect of a cowbird and the early hatching date of the young.

Survival of young.—The proportions of junco eggs that hatched and those that fledged (in broods in which at least one young fledged) were only slightly reduced in parasitized nests (Mann-Whitney U -test; $P > 0.1$) (Table 2). The absolute numbers, however, of junco young that hatched and fledged from parasitized nests were significantly reduced (one-tailed t -tests; young hatching, $t = 3.68$, $df = 37$, $P < 0.001$; young fledging, $t = 2.43$, $df = 18$, $P < 0.025$).

There was no difference during the nestling stage in the rate of complete nest predation between parasitized and nonparasitized broods (76% vs 64% of broods fledged, $\chi^2 = 0.66$, $P > 0.5$). Starvation occurred in only 2 nests in 1983; one was nonparasitized, and the other had 2 cowbirds (the only brood with 2 cowbirds). In another nest the cowbird apparently

crowded its 2 junco nestmates out of the nest over the course of 3 days. At this point the cowbird weighed more than twice as much as its junco nestmates.

The survivorship of the fledgling cowbirds could be determined adequately for only 6 families. In 2 of the broods the cowbird disappeared within 4 days after fledging, and in 4 broods it survived to independence (fledglings were considered independent after 15 days postfledging, when they were observed to feed themselves). Two of the surviving cowbird fledglings were the only fledglings remaining in their brood. The remaining two cowbird fledglings were raised in families with one and two junco fledglings, respectively.

DISCUSSION

Parasitism in relation to habitat and predation.—Overall parasitism and predation rates in this study were heavier in 1984 than in 1983; in 1984 parasitism and predation rates were greater in open habitats than in forested habitats. It seems possible that both cowbirds and predators may take advantage of the relative conspicuousness of nests in the more open areas. Yearly variation in the rate of parasitism in different habitats may result from fluctuations in either host availability or cowbird density (McGeen and McGeen 1968, Rothstein et al. 1984).

Nests of the Oregon race of the Dark-eyed Junco (*Junco hyemalis oreganus*) in the Sierra Nevada in California were parasitized almost exclusively in open meadow areas (White 1973). Similarly, parasitized Song Sparrow nests in Ohio tended to be less concealed than were nonparasitized nests (Nice 1937:162–163). Nest concealment apparently had no influence on cowbird parasitism in Song Sparrows breeding on Mandarte Island, British Columbia, (Smith 1981), or in Prairie Warblers (Nolan 1978:411).

Junco nests at MLBS contained cowbird eggs laid by one or two cowbirds, (as indicated by distinct types of cowbird eggs within a nest; Dufty 1983, Fleischer 1985). Radio-tracking studies have shown that although individual female cowbirds occupy home ranges that tend to be exclusive of other females (Dufty 1982, Rothstein et al. 1984), overlap in host nests does occur.

Cowbird reproductive success and the effect of cowbirds on junco reproductive success.—The reproductive success of Brown-headed Cowbirds, although lower than that of juncos, was evidently high compared with most cowbird populations studied (Scott and Ankney 1980); 57% survived during the nestling stage, and 67% of the fledglings survived to independence. This survivorship measure may have been increased because only a single cowbird nestling was present in any given junco nest. My removal of male juncos, however, may have confounded cowbird postfledging

survival. Cowbird mortality was apparently higher both in the Sierra Nevada (White 1973) and in British Columbia (Smith 1981). Woodward (1979) found that the highest mortality in cowbirds occurred during the first few days after fledging for several North American passerine hosts.

Fewer junco young hatched and fledged in parasitized than in nonparasitized nests, probably because of the removal of and damage to junco eggs by cowbirds (Friedmann 1929, Nice 1937:157, Hoy and Ottow 1964, Carey 1986). Once hatched, however, most junco nestlings raised with cowbirds appeared to fare as well as those in nonparasitized broods. Several interacting factors contributed to the variation in cowbird and junco nestling weight. In 1983 both cowbird and junco nestlings were heavier later in the season, and the presence of cowbirds combined with the absence of a male parent resulted in lower junco nestling weights. However, the fledging weight of juncos was not correlated with survival to independence (Wolf, Ketterson, and Nolan, unpubl. data). The mean number of independent junco young produced over the entire season by females hatching at least one parasitized brood was significantly less than for unparasitized females.

Possible antiparasite adaptations.—My findings suggest that cowbirds may be exerting a slight negative impact on the junco population in the Allegheny Mountains, even though the density of breeding juncos in this population appears to be similar to, if not higher than, the density found by Hostetter in 1936–1938 (1961) (5.0 nests/km then vs 12.4 nests/km now), well before cowbird invasion occurred (however, the higher number of nests in my study may be due to nests found in areas other than on the roads). Thus I consider below whether adaptations against brood parasitism may be incipient in this junco population (Rothstein 1975b).

Payne (1977) suggested 3 primary mechanisms that could reduce or avoid brood parasitism: (1) A shift in breeding season: The host breeds at a time during the season that circumvents that of the parasite. (Multiple-brooding is included in this category.) (2) Nest desertion or burial of eggs in the nest by building over. (3) Ejection of parasite eggs: This behavior is not known to occur in juncos and will not be considered further. A fourth possibility, vigilance toward the parasite at the nest site (Robertson and Norman 1976, Smith et al. 1984), was not assessed in this study, and I do not consider this possibility further.

Late-season broods may partly compensate for the decreased reproductive success suffered in early-season broods in Dark-eyed Juncos. As the probability of parasitism after mid-June decreases (Fig. 1), clutches initiated during this period are relatively cowbird-free. However, second and late clutches occurred even before cowbird invasion (Hostetter 1961), and thus cannot be considered a behavior selected for by parasitism.

In 1983 few females deserted their nests as a consequence of parasitism,

but desertions were more frequent in 1984 (i.e., when cowbirds had laid eggs or I had substituted cowbird eggs). Furthermore, most desertions occurred before the clutch was complete. These desertions may have been an evolved response to partial clutch reduction, caused either by cowbirds removing host eggs, or by predation (Wiley 1985, Rothstein 1986). Desertion of small clutches, especially early in the season, would allow the host to renest rapidly with a full clutch, thus maximizing its reproductive output.

Do Dark-eyed Juncos in southwest Virginia show antiparasite adaptations? Although some nest desertions of parasitized clutches did occur, alternate explanations (e.g., response to nest predation) are possible. As the reproductive success of juncos appeared to decrease as a result of brood parasitism, antiparasite adaptations would be expected to evolve (Rothstein 1975a). The apparent lack of antiparasitic behavior to date may be due to the fact that juncos have not been exposed to cowbird parasitism long enough for antiparasite adaptations to evolve. On the other hand, a high predation rate results in the destruction of most nests, and, perhaps, the combination of costs resulting from nest desertion or egg burial (in terms of breeding time and energy investment) and the small average impact of cowbirds on junco reproductive success exceeds the costs of avoiding parasitism. Thus, factors other than cowbird parasitism may have a greater influence on lifetime reproductive success (cf. Payne 1969, McGeen 1972, Smith 1981). In juncos and other species, high variability in parasitism pressure from year to year appears to be common (Mayfield 1960, Walkinshaw 1961, 1983, Nice 1937, McGeen 1972, Nolan 1978, Smith 1981). This variation may result in insufficient selective pressure for the evolution of antiparasite behavior. Experimental studies (cf. Rothstein 1975b, 1986) are needed to test whether antiparasite adaptations have indeed evolved in the Dark-eyed Junco.

ACKNOWLEDGMENTS

This research was supported by the Frank M. Chapman Memorial Fund, Indiana Academy of Science Research Grant, Indiana University Biology Department Breckenridge Fellowship, and the Mountain Lake Biological Station Pre-doctoral Fellowship. I wish to thank E. D. Ketterson, V. Nolan, and P. Sniegowski for discussion and helpful comments on several versions of the manuscript. J. Wolff, R. Mumme, W. Post, and S. I. Rothstein also contributed valuable criticisms.

LITERATURE CITED

- CAREY, C. 1986. Possible manipulation of eggshell of host eggs by Brown-headed Cowbirds. *Condor* 88:388-390.
- DUFTY, A. M., JR. 1982. Movements and activities of radio-tracked Brown-headed Cowbirds. *Auk* 99:316-327.

- . 1983. Variation in the egg markings of the Brown-headed Cowbird. *Condor* 85: 109–111.
- FLEISCHER, R. C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. *Behav. Ecol. Sociobiol.* 17:91–99.
- FRIEDMANN, H. 1929. The cowbirds. A study in the biology of social parasitism. Charles C Thomas, Springfield, Illinois.
- , L. F. KIFF, AND S. I. ROTHSTEIN. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. *Smithson. Contrib. Zool.* 235.
- HANN, H. W. 1937. Life-history of the Ovenbird in southern Michigan. *Wilson Bull.* 49: 145–237.
- . 1941. The cowbird at the nest. *Wilson Bull.* 53:211–221.
- HOSTETTER, R. D. 1961. Life history of the Carolina Junco. *Raven* 32:97–170.
- HOY, G. AND H. OTTOW. 1964. Biological and oological studies of the molotherine cowbirds (Icteridae) of Argentina. *Auk* 81:186–203.
- MAYFIELD, H. 1960. The Kirtland's Warbler. *Cranbrook Inst. Sci. Bull.* 40.
- . 1965. The Brown-headed Cowbird with old and new hosts. *Living Bird* 4:13–28.
- MCGEEN, D. S. 1972. Cowbird-host relationships. *Auk* 89:360–380.
- AND J. J. MCGEEN. 1968. The cowbirds of Otter Lake. *Wilson Bull.* 80:84–93.
- NICE, M. N. 1937. Studies in the life history of the Song Sparrow. *Trans. Linn. Soc. N.Y.* Vol. IV.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler (*Dendroica discolor*). *Ornithol. Monogr.* 26.
- PAYNE, R. B. 1969. Analyses of nesting mortality in birds. *Smithsonian Contrib. Zool.* 9: 1–48.
- . 1977. The ecology of brood parasitism in birds. *Ann. Rev. Ecol. Syst.* 8:1–28.
- ROBERTSON, R. J. AND R. F. NORMAN. 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. *Condor* 78:166–173.
- ROTHSTEIN, S. I. 1975a. Evolutionary rates and host defenses against avian brood parasitism. *Am. Nat.* 109:161–176.
- . 1975b. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250–271.
- . 1986. A test of optimality: egg recognition in the Eastern Pheobe. *Anim. Behav.* 34:1109–1119.
- , J. VERNER, AND E. STEVENS. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. *Ecology* 65:77–88.
- SCOTT, D. M. AND C. D. ANKNEY. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. *Auk* 97:677–683.
- SMITH, J. N. M. 1981. Cowbird parasitism, host fitness, and age of the host in an island song sparrow population. *Condor* 83:152–161.
- , P. ARCESE, AND I. G. MCLEAN. 1984. Age, experience, and enemy recognition by wild Song Sparrows. *Behav. Ecol. Sociobiol.* 14:101–106.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry*. Freeman, San Francisco, California.
- SOUTHERN, W. E. 1958. Nesting of the Red-eyed Vireo in the Douglas Lake region, Michigan. *Jack-Pine Warbler* 36:185–207.
- WALKINSHAW, L. H. 1961. The effect of parasitism by the Brown-headed Cowbird on *Empidonax* flycatchers in Michigan. *Auk* 70:266–268.
- . 1983. Kirtland's Warbler: the natural history of an endangered species. *Cranbrook Inst. Sci.*, Bloomfield Hills, Michigan.
- WHITE, J. M. 1973. Breeding biology and feeding patterns of the Oregon Junco in two Sierra Nevada habitats. Ph.D. diss., Univ. California, Berkeley, California.

- WILEY, J. W. 1985. Shiny Cowbird parasitism in two avian communities in Puerto Rico. *Condor* 87:165–176.
- . 1986. Growth of Shiny Cowbirds and host chicks. *Wilson Bull.* 98:126–131.
- WOODWARD, P. W. 1979. Survival of fledgling Brown-headed Cowbirds. *Bird Banding* 50: 66–68.

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS

The North American Bluebird Society announces the fifth annual grants in aid for ornithological research directed toward cavity nesting species of North America with emphasis on the genus *Sialia*. Presently three annual grants of single or multiple awards totaling \$7,500.00 are awarded and include:

J. L. Williams Memorial Bluebird Research Grant.—Available to student, professional or individual researchers for a suitable research project focused on any of the three species of bluebird from the genus *Sialia*.

General Research Grant.—Available to student, professional and individual researchers for a suitable research project focused on a North American cavity nesting species.

Student Research Grant.—Available to full-time college or university students for a suitable research project focused on a North American cavity nesting species.

Further guidelines and application materials are available upon request from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746. Completed applications must be received by December 1, 1987; decisions will be announced by January 15, 1988.

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANT AWARDS

The North American Bluebird Society is proud to announce the presentation of the fourth annual research grant awards. The 1987 recipients are as follows:

Bluebird Grant

Wayne H. Davis.—Eastern Bluebird and European Starling: Competition for Nest Sites. \$1125

Steven G. Parren.—Bluebird Nest Box Selection by Competing Passerines. \$950.

Student Grant

Danny J. Ingold.—Nesting Phenology and Competition for Nest Sites Among Red-headed and Red-bellied Woodpeckers and European Starlings in East Central Mississippi. \$400

Kimberly A. With.—Effects of Brood Size on the Parental Care of Western Bluebird Nestlings. \$836

General Grant

Vasiliki Demas.—Effect of Blowfly Parasitism on the Growth and Development of Western Bluebird Nestlings. \$1000

Gregory Hayward.—Potential of Nest Boxes for Monitoring and Managing Boreal Owls. \$1050

William McComb.—Microclimatic Characteristics of White-breasted Nuthatch Roost Sites. \$1110

The North American Bluebird Society annually provides research grants in aid for ornithological research directed toward cavity nesting species of North America with an emphasis on the genus *Sialia*. Information and application materials are available from Theodore W. Gutzke, Research Committee Chairman, P.O. Box 121, Kenmare, North Dakota 58746.